FEEDING OF OYSTERS IN RELATION TO TIDAL STAGES AND TO PERIODS OF LIGHT AND DARKNESS

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INTRODUCTION

The beds of the American oyster, *Ostrea virginica*, are usually situated in inshore areas where tidal currents are strong and their regularity is sharply defined. Because of an almost continuous flow of water generated by the tidal movements over the beds populated with oysters, these mollusks live under continuously changing conditions. There is no doubt that the environmental changes caused by the tides may in certain instances noticeably affect the behavior of the oysters. It has never been satisfactorily demonstrated, however, that some of the vital processes of oysters, such as feeding, are carried on more vigorously during certain stages of the tide.

A review of the literature on this subject shows that the only attempt to study the relation between the feeding activities of oysters and the stages of the tide was made by Nelson (1921) who came to the conclusion that "The times of complete cessation or of commencement of feeding shows a rather definite correlation with the stage of the tide." In his other article on the feeding habits of oysters Nelson (1923) states that in the case of these mollusks relatively little food is taken on the ebb tide. Even as late as 1938 Nelson still refers to his old observations emphasizing the relative inactivity of the oyster during the outgoing tide (Nelson, 1938). These conclusions were accepted without verification by some other investigators and were finally incorporated in the article on oysters in the Encyclopaedia Britannica where it is stated that "The American oyster does not feed late at night and in early morning, and relatively little on the ebb tide" (Orton, 1929). At present, therefore, such behavior of oysters is recognized as an established fact.

In our investigations of various aspects of the biology of oysters of Long Island Sound and its tributaries, especially of Milford Harbor, it was noticed that these mollusks fed actively on the ebb tide and also during darkness. The stomachs of the oysters removed from the water during such periods contained large quantities of food. It was also observed on numerous occasions in the day time that during the last stages of the ebb the oysters populating the shallow flats were wide open and apparently feeding because they were expelling true faeces. These observations suggested that the conclusions expressed by Nelson and Orton probably did not apply to the oysters of the Long Island Sound and Milford Harbor region. However, since our observations were only of an occasional nature, they could not be regarded as entirely reliable. Therefore, to ascertain the feeding habits of our oysters in relation to the tidal stages, and to the periods of light and darkness, a systematic series of experiments was conducted in the Summer and Autumn of 1945. The solution of the problem undertaken was approached by using several methods, each of which contributed toward the correct evaluation of the results of the others.

The authors wish to express their sincere appreciation and thanks to Miss Frances Tommers for her helpful participation in all the phases of this work and especially for the difficult analysis of numerous kymograph records obtained in the course of these studies.

Observations and Experiments

Stomach content

The first method consisted in examining the volume of the stomach content of the oysters collected during different stages of the incoming and outgoing tides. As a rule, the oysters examined were approximately 4 inches in length. The examination was made immediately after the specimens were taken out of the water. After opening an oyster an incision penetrating to the stomach was made through the body wall and the content of the stomach was collected by means of a fine pipette inserted through the incision.

At first it was intended to employ a volumetric method for determining the quantities of food found in the stomachs but, eventually, this method was found unsatisfactory because the bodies of the oysters, regardless of quite a uniformity of their shells, displayed considerable difference in their volume and size. Since small-bodied oysters possessed smaller stomachs and were probably incapable of ingesting quantities of food equal to those of larger individuals, serious errors could be introduced in the interpretation of the results. Therefore, another method, in which each oyster was considered individually, was decided upon. This method consisted in a direct evaluation of the relative quantity of food found in the oyster's stomach. Three classes, namely: "large," "small," and "absent," were established to designate the results of the examination. The oysters which were classified as containing large quantities of food could easily be recognized because, as soon as the incision was made in their bodies, the stomach content freely flowed out. This phenomenon is probably familiar to all investigators who worked with oysters. The animals placed in the second class were those whose stomachs contained only small quantities of food. The third class was composed of oysters with empty stomachs. The animals of the latter group were especially carefully examined to be certain that they contained no food.

The largest number of oysters examined in the course of these studies was collected from the cultivated oyster beds of Long Island Sound. This group, consisting of 1000 individuals, was composed of ten samples, each usually containing 100 oysters. These samples were collected at approximately weekly intervals during June, July, and August 1945. Each of the large samples consisted in turn of ten smaller ones composed of 8 to 12 individuals. The latter samples were dredged from our ten collecting stations established in the Sound. All these stations, located at a depth ranging from 10 to 30 feet at the mean low water stage, were subjected to strong tidal currents. The exact time of the collection of each sample was recorded and later correlated with the stage of the tide.

The collection of samples from all the stations extending along the shore for a distance of about 25 miles usually required from six to eight hours. Thus, it was sometimes possible to continue to collect samples during the entire period of the outgoing or incoming tide. The stations were not always attended in the same sequence to guarantee that the sampling was of a random nature.

The results of the examination of 1000 oysters offered rather conclusive evidence that the mollusks were feeding as actively on the ebb tide as they did during the flood (Table I). As a matter of fact, the per cent of oysters containing a large quantity of food was somewhat higher on the ebb than during the flood. Furthermore, only 6 per cent of the oysters collected during the ebbing tide possessed empty stomachs, while among the individuals dredged during the flood 10 per cent showed a complete absence of food. It is significant that among the oysters collected during the low water stage the per cent of the individuals containing a large quantity of food was higher, and that of the animals with empty stomachs lower than at many other stages of the tide. While this observation cannot be interpreted as definite proof that oysters feed most efficiently just prior and during the low water stage, it shows, nevertheless, that they do not cease, or noticeably decrease, their feeding activities during late ebb.

TABLE I

Relative quantities of food in stomachs of 1000 oysters collected at different tidal stages in Long Island Sound, June, July, and August 1945

Stage of tide	Oysters examined	Quantity of food			Per cent		
		Large	Small	Absent	Large	Small	Absent
Flood							
1st hour	41	31	6	4	75	15	10
2nd hour	60	51	2	7	85	3	12
3rd hour	85	58	9	18	68	11	21
4th hour	75	66	5	4	88	7	5
5th hour	85	72	8	5	85	9	6
High water	110	91	9	10	83	8	9
Total	456	369	39	48	81	9	10
Ebb							
1st hour	80	66	11	3	82	14	4
2nd hour	80	69	7	4	86	9	5
3rd hour	120	102	10	8	85	8	7
4th hour	90	76	10	4	85	11	4
5th hour	107	84	13	10	79	12	9
Low water	67	59	6	2	88	9	3
Total	544	456	57	31	84	10	6
Grand total	1000	825	96	79	82	10	8

Additional observations on the relative quantities of food in the stomachs of the oysters at the end of the flood and during the entire period of ebb were made in Long Island Sound on August 21, 1945. On that day a station was chosen in 20 feet of water on one of the beds planted with 4-year-old mollusks. The location of the station was designated by a special buoy. The samples were collected at hourly intervals beginning one hour prior to the high water stage (Table II). Altogether eight samples, each composed of 20 oysters, were collected and examined.

The salinity of the water ranged from 27.31 p.p.t. soon after high water to 25.45 p.p.t. at low water.

The results of the examination again showed that in the majority of the oysters the stomachs contained large quantities of food during all stages of the ebb (Table II). The observations also indicated that there was no decrease in the number of oysters with food-filled stomachs parallel with the falling of the tide. On the contrary, the largest number of oysters containing large quantities of food was found only one hour prior to low water.

It is significant that among the oysters examined during the last three hours of the ebb not a single individual was found with an empty stomach. While the presence of food in the oysters dredged during the early stages of the outgoing tide could be possibly explained by assuming that this food was ingested during the last

TABLE II

Relative quantities of food in stomachs of 160 oysters collected at hourly intervals during last hour of flood and during ebb from a station established in 20 feet of water in Long Island Sound, August 21, 1945. Each sample composed of 20 oysters.

Stage of tide	Temperature °C.	Quantity of food		
		Large	Small	Absent
Flood				
5th hour	21.2	11	8	1
High water	20.9	17	3	0
Ebb				
1st hour	21.1	14	6	0
2nd hour	21.0	19	1	0
3rd hour	20.9	17	2	1
4th hour	21.1	19	1	0
5th hour	20.6	20	0	0
Low water	20.4	16	4	0
Total		133	25	2

hour of flood, such an explanation cannot be offered for the presence of food in the oysters examined from three to six hours after the high water stage. Our observations performed under laboratory conditions on oysters kept in water of 20.0° C. showed that these mollusks pass the particles of food through their entire digestive system from 1 hour 20 minutes to approximately 2 hours and 30 minutes. Therefore, it seems rather improbable that the food found in the oysters during the latter part of the ebb was that ingested during the late stage of the flood, four to six hours prior to examination.

In general, the observations made on 160 oysters on August 21, 1945, showed that the oysters of Long Island Sound fed very actively during the ebb, and that the relative quantities of food found in their stomachs during that period were at least equal to or even exceeding those recorded during the last hour of the preceding flood.

Although observations in Long Island Sound have demonstrated that there was no correlation between the stages of the tide and the quantities of food found in the stomachs of the oysters, it was desirable to supplement the data already available with additional observations on the oysters living under ecological conditions rather different than those of Long Island Sound proper. An area in Milford Harbor near the dock used for laboratory needs, was chosen for these observations. A large number of oysters living on the bottom near the dock made such an arrangement especially convenient.

Milford Harbor was selected because it was a typical example of a small partially inclosed body of water where extensive natural beds had existed. In recent times many of the beds were destroyed by overfishing, and the profile of the bottom was markedly changed by the dredging of a wide and deep channel. Nevertheless, the oysters quickly reestablished themselves in more shallow sections of the Harbor, and at present are quite common. A good setting of oysters regularly occurs in the Harbor, indicating that the conditions are favorable for the propagation of these mollusks. Usually changes in the temperature and salinity of the Harbor water during the tidal cycle are more pronounced than in Long Island Sound proper, where both these factors remain very steady (Loosanoff and Engle, 1940).

The observations consisted in examining the stomach content of the oysters at hourly intervals throughout a 24-hour period. The samples, each composed of six individuals, were suspended one day prior to the beginning of the examination in baskets made of 2-inch mesh poultry wire. All the baskets were kept at the same depth, namely, one foot below the mean low water line. They were separated from each other by a distance of approximately one foot and, therefore, the removal of any of the baskets did not disturb the oysters of the other containers. The experiment continued from 7:30 A.M. of July 27 until 8:00 A.M. of July 28, covering three low and two high water stages, and including periods of light and darkness (Table III). During this period the temperature of the water ranged from 22.0 to 25.0° C., the salinity fluctuated between 22.68 and 28.44 parts per thousand, and the pH from 7.7 to 8.7.

The data obtained indicated that during the two flood and two ebb periods covered, the majority of the oysters contained large quantities of food. Of the total number of 150 oysters examined 86 per cent belonged to that group. This figure closely approached that for the Long Island Sound oysters where 82 per cent were found to possess large quantities of food (Table I). Only 4 per cent of the Milford Harbor oysters were found with empty stomachs, the figure being too low to suggest that large groups of the oyster population ceased feeding for appreciatively long intervals during the period of observation.

More detailed studies of the data given in Table III do not offer sharply defined evidence which would lead to the conclusion that the oysters collected during the flood contained more food than those collected at ebb, or vice versa. Although it is true that all but one oyster collected during the second flood period, extending from 8:40 P.M. to 1:58 A.M., contained large quantities of food, virtually the same observations were made during the preceding period of ebb when 32 out of 36 oysters showed full stomachs. In each case only one oyster with an empty stomach was found. If the condition of the oysters during the first flood period (8:30 A.M. to 1:30 P.M.) is compared with that of the oysters examined during the second ebb period (3:00 A.M. to 8:00 A.M.), it will be found that in each case 28 individuals showed large, and 6 showed small quantities of food, while 2 oysters were with empty stomachs.

TABLE III

Temperature, salinity and pH of the water, and relative quantities of food in stomachs of oysters examined at hourly intervals during a 24-hour period in Milford Harbor on July 27 and 28, 1945. Each sample of oysters consisted of six individuals.

Stage of tide	Time of day	Temperature °C.	Salinity p.p.t.	pH	Quantity of food			Stage of tide	Time of day	Temperature °C.	Salinity p.p.t.	pH	Quantity of food		
					Large	Small	Absent						Large	Small	Absent
Low water	7:30 A.M.	24.2	22.68	7.7	6	0	0								
Flood								Flood							
1st hour	8:30 A.M.	24.0	27.74	7.7	4	2	0	1st hour	8:45 P.M.	24.5	24.40	8.7	6	0	0
2nd hour	9:30 A.M.	23.2	26.59	8.0	3	2	1	2nd hour	9:45 P.M.	23.9	25.73	8.5	6	0	0
3rd hour	10:30 A.M.	23.3	27.65	8.0	6	0	0	3rd hour	10:45 P.M.	23.3	26.00	8.5	6	0	0
4th hour	11:30 A.M.	23.0	28.44	8.0	3	2	1	4th hour	11:40 P.M.	23.3	26.00	8.5	5	0	1
5th hour	12:30 P.M.	23.1	27.65	8.1	6	0	0	5th hour	12:45 A.M.	23.1	26.54	8.5	6	0	0
High water	1:30 P.M.	23.1	26.33	8.2	6	0	0	High water	1:58 A.M.	23.0	26.27	8.5	6	0	0
Ebb								Ebb							
1st hour	2:30 P.M.	23.2	27.65	8.2	6	0	0	1st hour	3:00 A.M.	23.0	26.00	8.5	5	0	1
2nd hour	3:30 P.M.	23.0	28.51	8.3	6	0	0	2nd hour	4:00 A.M.	23.1	26.27	8.5	6	0	0
3rd hour	4:30 P.M.	23.4	26.39	8.3	4	2	0	3rd hour	5:00 A.M.	23.3	26.27	8.4	4	2	0
4th hour	5:30 P.M.	23.9	26.13	8.3	5	0	1	4th hour	6:00 A.M.	23.0	25.73	8.1	3	2	1
5th hour	6:30 P.M.	24.9	24.52	8.1	5	1	0	5th hour	7:00 A.M.	23.2	25.47	8.1	5	1	0
Low water	7:40 P.M.	24.7	24.13	8.4	6	0	0	Low water	8:00 A.M.	23.4	25.47	8.0	5	1	0
								Total					129	15	6
								Per cent					86	10	4

Perhaps it should be emphasized that among the 18 animals collected at the three low water stages (Table III) all but one oyster had large quantities of food in their stomachs.

Studies of the same nature as those made on July 27 and 28 were performed again on August 9. However, in the latter case observations were made only during one flood and one ebb stage covering a period of about 12 hours. The results of the observations are incorporated in Table IV together with data on the water temperature, salinity and pH recorded at the collection of each sample. The results showed that more oysters with large quantities of food were found in the group collected during the ebb than among the animals examined during the flood. However, no significant difference was noted between the two groups in the number of oysters with empty stomachs.

TABLE IV

Relative quantities of food in oysters examined at hourly intervals during a 12-hour period in Milford Harbor on August 9, 1945. Each sample composed of 6 oysters. Temperature, salinity and pH are indicated for each stage of the tide.

Stage of tide	Time of day	Temperature °C.	Salinity p.p.t.	pH	Quantity of food		
					Large	Small	Absent
Flood							
1st hour	7:55 A.M.	22.2	24.99	7.9	0	5	1
2nd hour	8:55 A.M.	21.9	25.72	7.9	1	5	0
3rd hour	9:55 A.M.	21.6	25.72	7.9	3	3	0
4th hour	10:55 A.M.	21.6	25.99	7 9	3	1	2
5th hour	11:55 A M	21.8	25.44	7.9	6	0	0
High water	12:55 P.M.	21.7	25.72	7.9	5	1	0
Total					18	15	3
Ebb							
1st hour	1:55 P.M.	22.0	25.72	8.0	4	2	0
2nd hour	2:55 P.M.	21.8	25.72	8.1	3	2	1
3rd hour	3:55 P.M.	22.0	25.72	8.1	6	0	0
4th hour	4:55 P.M.	23.9	25.44	8.1	6	0	0
5th hour	5:55 P.M.	24.4	23.84	8.0	4	2	0
Low water	7:05 P.M.	25.1	21.44	8.0	6	0	0
Total					29	6	1

In summarizing all our observations on the relative quantities of food present in the stomachs of the oysters during different tidal stages the conclusion may be formed that, as far as ingestion of food is concerned, the oysters of Long Island Sound and Milford Harbor do not show a definite preference either to ebb or to flood. During either stage the predominating majority of the oysters contained large quantities of food, whereas individuals with empty stomachs were found only occasionally. The data obtained fail to lend any support to the unqualified opinion that the American oyster, *O. virginica*, takes relatively little food on the ebb tide.

Rate of water pumping in relation to tide

To determine the rate of water pumping of oysters and, therefore, the efficiency of their feeding at different stages of the tide an apparatus was constructed which permitted the measurement of the actual quantities of water passing through an oyster (Fig. 1). This apparatus was installed on the edge of the dock situated along the western shore of Milford Harbor where a swift tidal current flowed unobstruct-

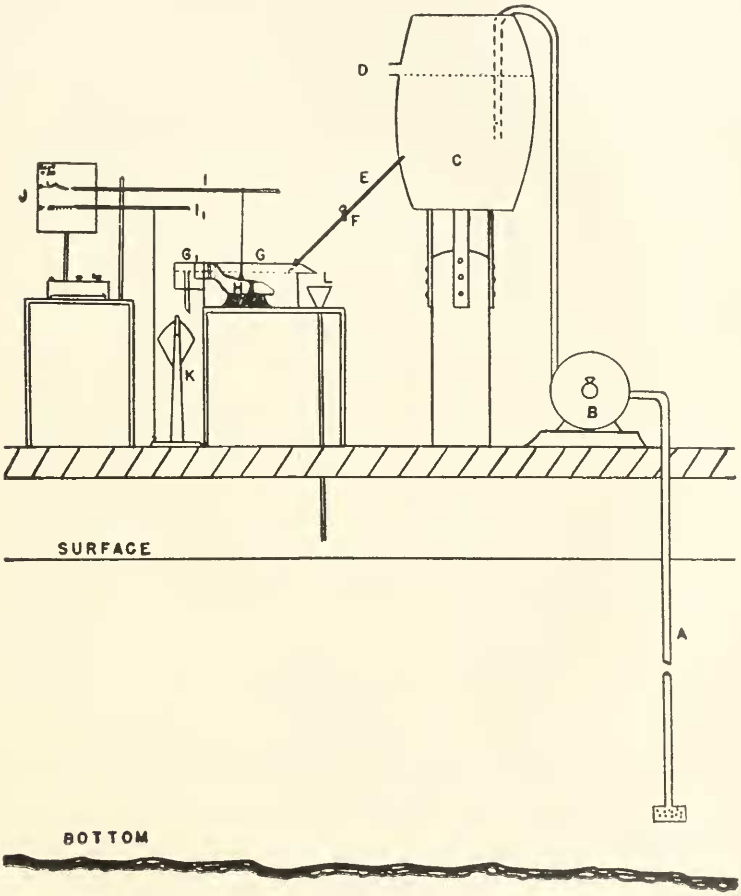

FIGURE 1. Diagram of the apparatus used in determining the quantities of water pumped by the experimental oysters. Description in text.

edly. The water supply was obtained through the hose, *A*, being pumped by the pump, *B*, into the storage barrel, *C*. The intake end of the hose, protected by a screen of large mesh always remained in the same position, six inches above the bottom. A constant water level in the barrel, *C*, was maintained by allowing the excess water to escape through the overflow outlet, *D*, to which a length of hose was attached. The capacity of the pump was such that the water in the storage barrel was renewed every 4 or 5 minutes. Thus, the experimental oysters were receiving water, which was changing parallel with the changes of the tide.

The water was fed to the experimental oysters through the tube, *E*, provided with a flow-adjusting cock, *F*. The constant level oyster chamber, *G*, contained the oyster, *H*, the excurrent side of which was covered with a rubber, cone-shaped apron which conducted the water pumped by the oyster into the smaller chamber, G_1. Moore (1908) and Nelson (1936) were the first to apply the rubber apron, while Galtsoff (1926) devised and began to use the chamber. A string glued to the upper shell of the oyster was attached to the counter-balanced lever, *I*, which recorded every movement of the shell on the kymograph, *J*.

The water pumped by the oyster into the chamber, G_1, overflowed through the glass tube standpipe into the tripping vessel, *K*, of known capacity. When the vessel was filled with the water pumped by the oyster it tripped over, emptying its contents, and at the same time striking a string attached to the lever, I_1, which made a mark on the kymograph, *J*. Thus, each tripping was recorded, and because the capacity of the vessel was known, the quantity of water pumped by the oyster during certain intervals could be ascertained easily. The excess water entering the chamber, *G*, but not utilized by the oyster flowed out through the outlet, *L*. The part of the experimental apparatus containing the oyster chambers and the kymograph was kept in a small shed to protect the oyster from the effects of the sun and from possible disturbances caused by the wind.

The oysters were placed in the apparatus usually from one to two hours before high or low water. This time was allotted to the oysters to open their shells and to begin pumping water at a normal rate. This introductory period was not included in the analysis of the pumping activities of the oysters.

At the end of the introductory period, which usually coincided with the high or low water stage, observations were carried on for 12 or 13 hours, covering one ebb and one flood stage. In this manner records of 27 oysters were obtained. Fortunately, in almost all cases the oysters remained open continuously throughout the period of exposure. The experiments were conducted at temperatures ranging from 19.1 to 25.8° C., a range considered very favorable for the pumping activities of oysters (Galtsoff, 1928).

In analyzing the kymograph records obtained in the course of these studies it was found convenient to divide each flood or ebb period into six hourly subperiods. However, since the ebb and flood periods of Milford Harbor are not usually of exactly 6-hour duration, the data for the last hour of each stage had to be arrived at by determining the quantity of water pumped by the oyster from the end of the fifth hour until the change of the tide and then calculated for a 60-minute period.

Analysis of the data showed that, in general, the rate of pumping of the oysters during the flood stages was somewhat slower than that during the ebbing periods (Table V). However, because of significant differences in the rate of pumping shown by individual oysters within the same hour of a tidal period, and after considering all the aspects of the data secured the opinion was formed that the oysters of Milford Harbor feed actively at all stages of the tide, and that the rate of feeding during the ebb is at least equal to and sometimes may be even more rapid than during the flood.

In Milford Harbor the strongest tidal currents occur in the middle of the period between the high and low water stages. This period, therefore, corresponds to the third and fourth hours of each stage. There is no evidence, nevertheless, that during this period the pumping of the oysters was more energetic than during the preceding or successive periods (Table V). It is of interest to note, however, that during the two last hours of the ebb the rate of pumping was somewhat accelerated.

The rapid rate at which many of the experimental oysters pumped water during ebb is well demonstrated in the photograph of the kymograph record showing the rate of pumping and shell movement of one of the experimental animals (Fig. 2). The period of observation lasted from 9:34 A.M. until 10:13 P.M., September 12, covering one complete flood and ebb period. Each vertical line of the lower record was made by the tripping vessel (Fig. 1), the capacity of which was 255 cc. Examination of the lower part of the record, which, incidentally, was made with the help of a dissecting microscope, a method always employed when the pumping was rapid and the marks on the kymograph were made close to each other, provided the following information: the minimum quantity of water pumped by the oyster during a single hourly period of the flood was 4080 cc., and the maximum, 20,655 cc. The average hourly rate of pumping for the entire flood period was 13,260 cc. For the ebb period these figures were 15,810, 23,715, and 20,244 cc. respectively.

TABLE V

Mean of quantities of water (in cubic centimeters) pumped by oysters during each hour of the flood and ebb periods. The data are based on the kymograph records of 27 oysters, Milford Harbor, Summer of 1945.

Stage of tide	Mean	Stage of tide	Mean
Flood		Ebb	
1st hour	15,952±1,214	1st hour	15,384± 787
2nd hour	14,411±1,578	2nd hour	15,962± 830
3rd hour	12,875±1,427	3rd hour	16,186±1,021
4th hour	12,470±1,389	4th hour	17,458±1,195
5th hour	13,438±1,130	5th hour	17,916±1,063
6th hour	14,131±1,040	6th hour	17,577± 941

Examination of other records of the same series revealed that during the ebb some of the oysters averaged from 25 to 27 thousand cc. per hour, while the maximum rate of pumping in some instances ranged from 31 to 34 thousand cc. per hour. Having in possession a large number of kymograph records of this nature one may well be inclined to disagree with the opinion that the American oyster is relatively inactive during the outgoing stage of the tide.

In connection with this discussion an interesting deduction can be made concerning the efficiency of the pumping mechanism of oysters. The average weight of the oyster meat removed from the shell the length of which is 4 inches is approximately 20 grams and its volume is usually not more than 20 cc. This organism, nevertheless, is capable of pumping 30 thousand cc. or more of sea water per hour. In other words, the volume of water passing through the oyster gills in one hour may be more than 1500 times greater than the volume of the oyster's body, a fact well attesting the efficacy of the feeding mechanism of this mollusk.

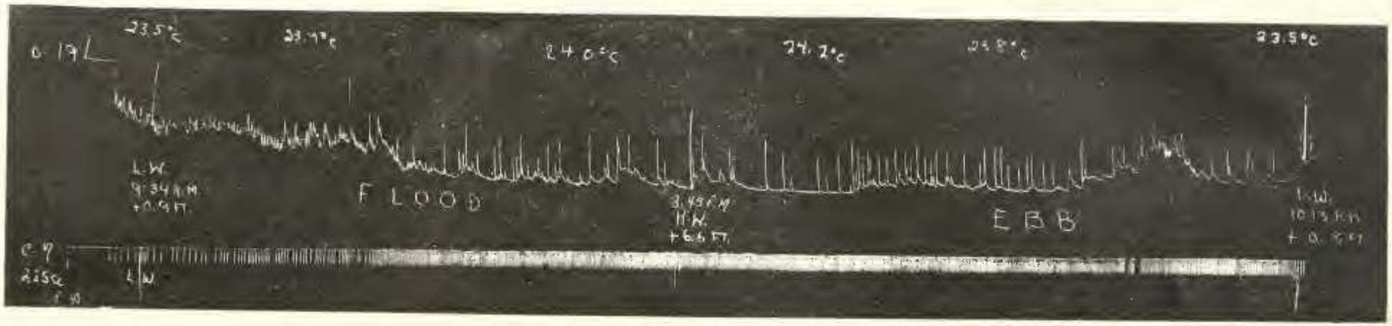

FIGURE 2. Photograph of kymograph record showing the shell movements (upper line) and rate of pumping (lower line) of oyster no. 19 obtained during the flood and ebb stages in Milford Harbor on September 12, 1945. Each vertical line of the lower record designates emptying of the tripping vessel (Fig. 1) of 255 cc. capacity. *L. W.* and *H. W.* indicate the low water and high water stages respectively.

Opening and closing of shells in relation to tide

Experiments for determining the presence or lack of correlation between the opening and closing of the oyster shells in relation to the tidal stages were also conducted in the Summer of 1945. The method used was the same as that successfully employed in the studies of the shell movements of hard shell clams, *Venus mercenaria*, and of the edible mussel, *Mytilus edulis* (Loosanoff, 1939, 1942). A description of this apparatus has already been published in full (Loosanoff, 1939) and, therefore, need not be repeated. It will be sufficient to say that this apparatus permitted registering on the Foxboro recorder of every shell movement of oysters kept under virtually natural conditions on the platform installed on the small oyster bed existing on the bottom of Milford Harbor. Even at low tides the experimental oysters were covered with at least 2 feet of water.

The area where the apparatus was installed was subjected to strong tidal currents which, during the spring tides, attained a velocity of 1.2 feet per second on the flood, and 1.5 feet per second on the ebb. During the neap tides, however, the velocity of the flood current was only 0.8 foot per second, and that of the ebb current, 1.3 feet per second. The mean range of tide in Milford Harbor is 6.6 feet, but during the spring tides high water occasionally reaches the 9-foot mark. In Milford Harbor, the same as in Long Island Sound, the strongest tidal currents occur in the middle of the period between high and low water. The slack usually coincides with the time of the high and low water stages.

Usually the records of two oysters were taken simultaneously—each record covering a 24-hour period. The temperature of the water was also continuously registered by Brown's recording thermometer which was installed near the shell movement recording apparatus, the bulb of the thermometer being only 5 inches away from the experimental oysters. The temperature range extended from 17.0 to 28.0° C., averaging approximately 22.0° C. Altogether 64 records of 18 different oysters were obtained in the course of these observations.

That the conditions in the Harbor were favorable for the existence of the mollusks was well shown by the growth of the young oysters which attached themselves to the concrete base of our apparatus used for studying the shell movements of the experimental animals (Fig. 3). The attachment, or, as it is more commonly called, the setting of the oysters took place early in August, soon after the apparatus was first placed in the water. The examination made late in September showed that the young oysters grew very well, regardless of the fact that the base was often removed from the water for short periods to change the experimental mollusks. This rapid growth of the young oysters, as well as their generally good condition, indicated that the experimental animals, the shell movements of which were recorded, were also subjected to favorable environment.

Analysis of 64 complete records showed that on an average the oysters remained open 22 hours and 39 minutes, or 94.3 per cent, and closed 1 hour and 21 minutes, or 5.7 per cent of a 24-hour period. Our figure for the duration of openness of the oyster shells is quite close to that of Nelson (1921) who, basing his conclusions on the records of 3 oysters, found that these animals remained open on an average of 20 hours per day, but is much higher than that offered by Galtsoff (1928) who found that the average period the oysters remain open is 17 hours and 7 minutes per day. However, the difference between Galtsoff's figures and ours may be explained on the basis that his observations were made on the oysters placed in the aquarium, while our animals were kept on the bottom of the Harbor, where conditions were different from those of the laboratory. Nevertheless, Galtsoff expresses the opinion, which coincides with ours, that oysters have a tendency to keep the shells open as long as possible.

Further statistical studies of the data collected showed that during the periods of flood the shells of the oysters remained open on an average of 93.4 per cent of the

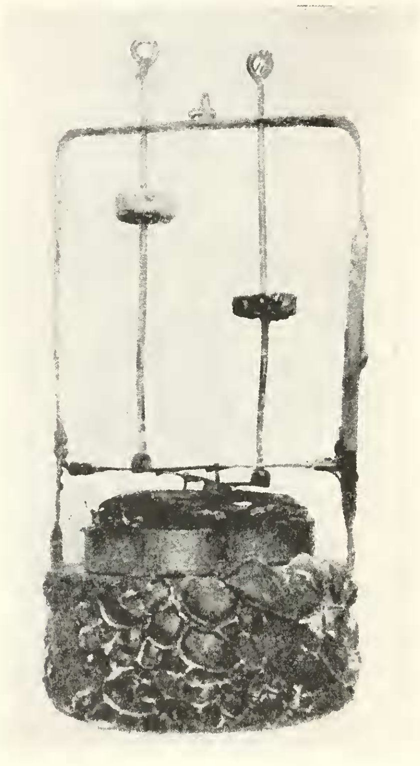

FIGURE 3. Photograph of the base of the instrument employed to record the shell movements of the oysters kept on the bottom of Milford Harbor. Note the healthy and vigorously growing young oysters attached to the sides of the base. Large experimental oysters imbedded in small concrete blocks can be seen on the top of the base.

time, whereas during the ebb periods the shells were open 95.2 per cent. Obviously, the difference between the two figures is rather insignificant, indicating that the behavior of the oysters is quite similar during the opposite stages of the tide.

Another trait of similar behavior of the oyster during the two different tidal stages was indicated by the fact that almost an equal number of records showing that the animals kept their shells open 100 per cent of the time was obtained for each stage. Thirty-three such records were made during the flood periods, and 32, during the ebb

Feeding in relation to time of day

While conducting these studies the opportunity presented itself to verify the statements that the feeding of oysters is considerably slowed down (Nelson, 1921, 1923) or entirely ceases (Orton, 1929) at night and in the early morning. The material for studying this problem was available from all three phases of our investigation, namely, observations on the stomach content of oysters, rate of pumping, and opening and closing of the shells.

Examination of the stomach content of the oysters made at hourly intervals during a 24-hour period in Milford Harbor on July 27 and 28, 1945, has shown that during the period of darkness, which extended from 8:33 P.M. until 5:33 A.M. (E.W.T.), the oysters contained as much food as during the hours of light (Table III). During the largest part of the period of darkness, until 5:00 A.M., almost all the oysters contained large quantities of food. The percentage of individuals with full stomachs during this period would compare favorably with that of the animals examined during the daytime. Numerous other examinations of the stomach content of the Milford Harbor oysters made between 1:00 and 6:00 A.M. during the Summer of 1945 also showed that the majority of the oysters had full stomachs. Obviously, these observations do not offer any support to the conclusion that oysters do not feed at night.

The results of the experiments in which the rate of pumping of the oysters was determined also contradict the above mentioned conclusion. Observations performed at night showed that the oysters remained active and fed very vigorously. The results of the experiment conducted during the night of July 27–28 were especially significant because in that case the period of late night coincided with the ebb (Fig. 4). Thus, the effects of two presumably unfavorable factors were combined. Nevertheless, as is shown in Figure 4, both experimental oysters remained open and continued to pump water at a very rapid rate during the entire period of darkness. When one of the animals closed at about 6:30 A.M. it already was one hour after sunrise. During the period of darkness the average rate of pumping of oyster no. 92 (upper record) was 17,934 cc. per hour, and the maximum, 19,272 cc. per hour. For oyster no. 98 (lower record) these figures were 24,622 and 30,600 cc. respectively.

Because this experiment was of a 24-hour duration data were also available on the rate of pumping of the same two oysters in daylight. The average rate of pumping of oyster no. 92 during that period was found to be 12,684 cc. per hour, and the maximum, 19,053 cc. per hour. For the second oysters the corresponding figures were 24,565 and 31,875 cc. Thus, in this case, the same as in the case of studies of the stomach content of the oysters, the conclusion may be offered that oysters feed actively during darkness. Furthermore, the average rate of pumping at night was not lower than during the daytime.

A series of supplementary experiments on the effect of light and darkness upon the rate of pumping also failed to show a significant difference in the behavior of oysters. These experiments were conducted in a dark room, where an apparatus of the type shown in Figure 1 was installed. Three or four oysters were tested simultaneously. During the period of light the oysters were illuminated with small floodlights. The intensity of light at the surface of the oysters, as determined by the Weston photronic exposure meter, was in excess of 1000 candles per square foot.

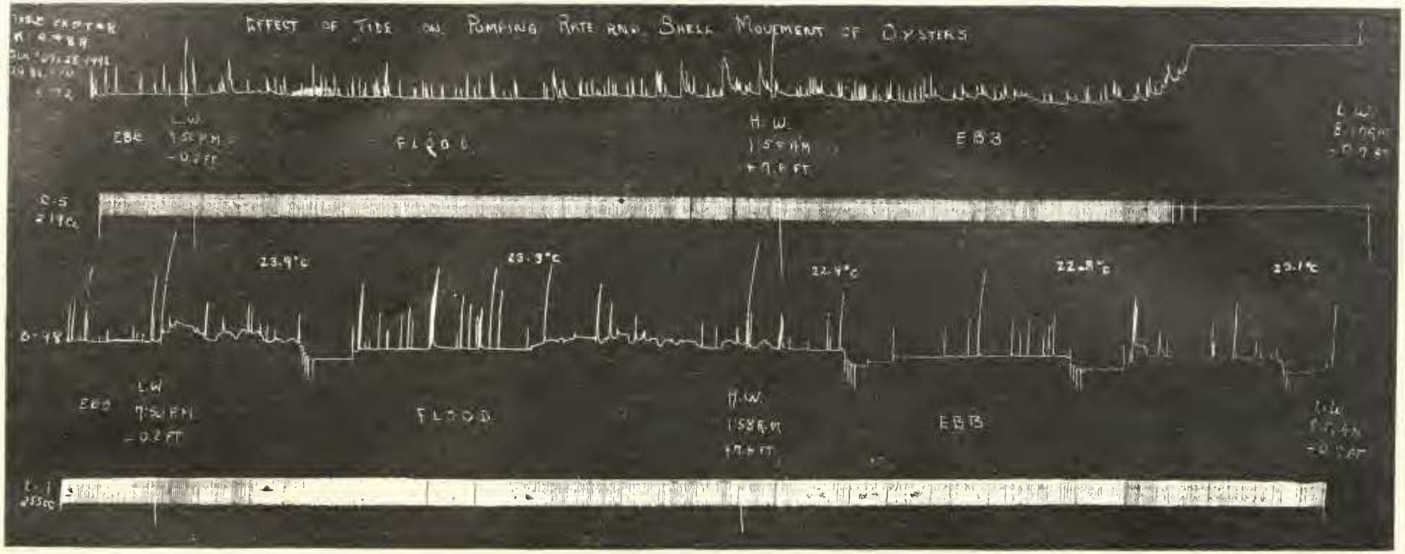

FIGURE 4. Photograph of the kymograph record showing the shell movements (1st and 3rd lines) and the rate of pumping (2nd and 4th lines) of two oysters during the period extending from 7:50 P.M., July 27 until 8:17 A.M. July 28, 1945. Each vertical mark of the second line designates emptying of the tripping vessel of 219 cc. capacity, while each mark of the fourth line shows the dumping of 255 cc. of water. The records show that both oysters fed very actively during the period of darkness, which extended from 8:33 P.M. until 5:33 A.M. *L. W.* and *H. W.* indicate the low water and high water stages respectively.

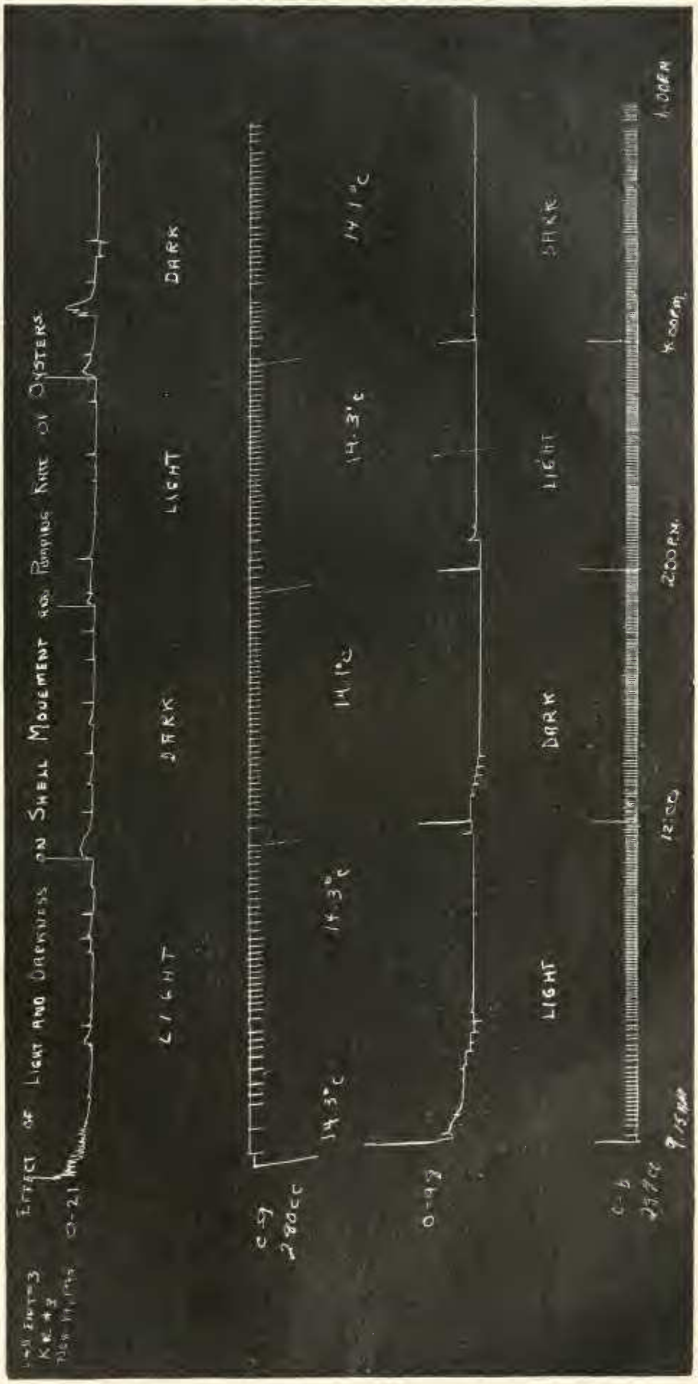

FIGURE 5. Photograph of kymograph record showing the shell movements (1st and 3rd lines) and the rate of pumping (2nd and 4th lines) of two oysters exposed to alternating periods of light and darkness. Each vertical mark of the second line designates the emptying of the tripping vessel of 280 cc. capacity, while each mark of the fourth line shows the dumping of 237 cc. of water.

The oysters were kept in the apparatus for approximately 9 hours (Fig. 5). During this time the mollusks were exposed to two periods of light and two of darkness. However, the initial period, of approximately 3 hours, was not included in the analysis, as this time was given to the oysters to become accustomed to the experimental condition. To equalize the data half of the experiments began with a period of light, and the other with that of darkness. Altogether 30 records of 10 different oysters were obtained. Analysis of the data showed that the mean hourly rate of pumping during the periods of light was 5350 ± 445 cc. For the periods of darkness this figure was 5036 ± 385. Thus, the rate of pumping during periods of light closely resembles that during periods of darkness.

Finally, the data on the same subject were taken from our 64 daily records of the shell movements of oysters. Analysis of these data showed that on an average the shells of the oysters remained open 94.4 per cent of the total time during daylight, and 93.8 per cent during the periods of darkness. The difference of less than one per cent is not considered as significant in this case, and, therefore, it may be concluded that in our experiments no correlation was found between the periods of closure of the shells and darkness. These results are in agreement with those of Galtsoff (1928) who in his article disagrees with Nelson's (1921, 1923) conclusion that the period of darkness, between 11:00 P.M. and 4:30 A.M., should be considered as a time of rest for oysters.

Discussion

The advocates of the opinion that oysters considerably reduce their feeding activities during the periods of ebb failed to suggest in their publications any factors which could be considered as responsible for the change in the behavior of the mollusks. It could be easily understood that in some areas, where the periods preceding and coinciding with the low water stage are accompanied by distinctly unfavorable changes in the environment, the oysters would temporarily slow down or even cease feeding. For example, a sharp decrease in salinity could compel the oysters to be relatively inactive. However, according to Nelson (1921) the reduction in salinity was not the cause. This conclusion is based upon his statement that in Huey's Creek, where the experiments were conducted, the periods of complete cessation or of the commencement of feeding, although showing a definite correlation with the stage of the tide, occurred independently of the changes in the density of the water, because such changes were usually of small magnitude.

Changes in the turbidity and temperature of the water were also considered as unimportant by Nelson (1923), who concluded that "The rate of filtration of water during any given period of time, as deducted from the rapidity and extent of ejections of accumulated sediment from the mantle cavity, may vary widely independently of the temperature and the turbidity of the water." In the same article Nelson also stated that "No correlation could be shown between the food content of the water and the periods of inactivity of the oyster." All these conclusions were based upon the experimental data first reported by Nelson in 1921. Thus, according to that author, neither changes in salinity or temperature, nor changes in the turbidity or quantity of food present in the water affected the rate of feeding of oysters. Yet, because of some undetermined factors these mollusks fed much less actively during the ebb stages.

In discussing Nelson's (1921) work it is necessary to mention that his experiments were devised to study the shell movements of the oysters, but not the rate at which these mollusks were filtering water through the gills, i.e., feeding. Only the shell movements of the oysters were recorded on the kymograph, while no data were obtained on the quantities of water pumped by the oysters during the different tidal stages. Obviously, no definite conclusions could be formed concerning the latter subject because of the almost complete lack of experimental evidence regarding this matter.

Nelson's method of interpreting the data should also be mentioned. In analyzing his material on shell movement of the oysters Nelson (1921) takes into consideration only the numbers of openings and closures of the shells during the different tidal periods. This method has already been criticized by Galtsoff (1928) who stated that "The examination of the number of closures and openings occurring during a given period of time does not convey a true idea of the activity or inactivity of the oyster. A better understanding can be gained by counting the number of hours the oyster was closed or open during a given period of a day." Obviously, Galtsoff's suggestion is well founded.

Our observations and experiments supplied the evidence that the oysters of Long Island Sound and Milford Harbor fed actively during the flood and ebb periods, and that during the ebb their feeding was often more energetic than during the flood. Observations of this nature could probably be made in many other bodies of water where changes in the tides are not accompanied by pronounced ecological changes. This conclusion appears to be logical because it is quite improbable that, if other conditions of the environment remain favorable, a change in the direction of the tidal current alone would affect the oysters. It is, to a certain extent, supported by our experiments in which pairs of oysters, employed in our studies of the shell movements, were always placed so that the hinges of their shells pointed in opposite directions. Thus, while the gills of one oyster faced the flood, the gills of the other animal were turned away from the direction of the current. Yet, no difference suggesting that an oyster in a certain position was more active on the flood or ebb was generally noted.

No correlation between the rate of water pumping of the oysters and the time of day was demonstrated by our experiments. Neither was it found that the duration of the opening and closure of the shells was affected by periods of light or darkness. In nature many oyster beds are located at a considerable depth. Very often the water flowing over the beds contains large quantities of suspended matter which stop the penetration of a large quantity of light before it reaches the bottom on which the oysters live. These oysters, therefore, normally exist in near-darkness even during very strong daylight. It is very doubtful that if other conditions remain favorable, the slight change in the intensity of illumination caused by the approach of night could have such a pronounced effect on the oysters that they would either begin to feed at a much slower rate or stop feeding entirely.

If the rate of feeding of oysters were markedly decreased during the nights and during the ebb periods, the existence of these mollusks would be under a rather unfavorable condition. Because the periods of darkness are often followed by ebb, there would be times when the feeding activities of the oysters would be continuously depressed for a period of approximately 18 hours. This condition would occur in September and October when the nights become long. However, it is a well known fact that during these two months the oysters of our waters undergo very rapid improvement in condition storing large quantities of glycogen in their bodies. Naturally, such an improvement could not be possible if, during this time of the year, the oysters had to exist under the conditions compelling them to be relatively inactive during approximately 12 hours of darkness and also during the 6 hours of ebb, a total of 18 hours per day.

As may be seen from this discussion, our conclusions regarding the activities of oysters during ebb and during periods of darkness do not agree with those of Nelson and Orton (ref. cit.). However, as Dr. Nelson suggests in recent personal communication with the senior author, the cause of the divergence may be attributed to the marked reduction of the pH during ebb and at night in the waters where Nelson's experiments were conducted. During the outgoing tide those areas received large quantities of swamp water which noticeably lowered the pH. Also, according to Nelson "These waters are but slightly buffered; hence at night with the respiration of algae and of animals and decomposition the water may become acid by morning." Such changes are indicated in one of Nelson's reports (1924). The conditions, however, are different in other basins, such as in many sections of Chesapeake Bay (Loosanoff, 1932) and Long Island Sound (Loosanoff and Engle, 1940) where the pH does not closely approach the neutral point.

In general, our experiments have shown that under favorable conditions neither tidal changes nor changes in the time of day affect the rate of feeding of oysters of Milford Harbor and Long Island Sound. Although the differences in the behavior between the individual oysters are of considerable magnitude, these mollusks, nevertheless, appeared to be feeding all or most of the time their shells remained open which, with a temperature range from 17.0 to 28.0° C., was approximately 94 per cent of the total time.

In presenting the final conclusions it should be once more emphasized that we do not interpret our results as applicable to all oyster growing areas of this coast. While our observations hold true for the areas where the experiments were conducted, and also, probably, for the waters where the ecological conditions resemble ours, it is realized that in other basins, where during ebb the oysters are exposed to unfavorable environment, different conditions may prevail. Nevertheless, the material presented in this article clearly indicates that the conclusions of Nelson (ref. cit.), which, no doubt, are representative for Huey's Creek, should not have been generalized and presented as applicable to the American oyster as a species (Orton, 1929).

Summary

1. Examination of approximately 1400 oysters collected during the different tidal stages in Long Island Sound and Milford Harbor failed to show any definite period when the stomachs of these mollusks displayed absence of food.

2. During all hours of the flood and ebb, including the low water period, the predominating majority of the oysters contained large quantities of food, whereas individuals with empty stomachs were found only occasionally.

3. The relative quantities of food found in the oyster stomachs during the ebb period were at least equal to or sometimes even exceeded those recorded during the flood.

4. Analysis of the kymograph records of the rate of water pumping by the oysters showed that they fed very actively at all stages of the tide, and that the rate of feeding during ebb was at least equal to or sometimes even more rapid than during the flood stage.

5. During the ebb some of the oysters pumped on an average of 25,000 to 27,000 cc. of water per hour, while the maximum rate of pumping in some instances ranged from 31,000 to 34,000 cc. per hour.

6. The efficiency of the feeding mechanism of an oyster may be well attested by the fact that the volume of water passed during one hour through the oyster gills may be more than 1500 times greater than the volume of the oyster's body.

7. Within the temperature range of 17.0 to 28.0° C. the oysters remained open on an average of 22 hours and 39 minutes, or 94.3 per cent, and were closed 1 hour and 21 minutes, or 5.7 per cent of a 24-hour period.

8. During the periods of flood the shells of the oysters remained open on an average of 93.4 per cent of the time, whereas during the ebb periods the shells were open 95.2 per cent.

9. During the periods of darkness the percentage of oysters with full stomachs was comparable to that of the individuals examined during the day time.

10. During darkness the oysters were found feeding very actively. The average rate of pumping at night was not lower than during the daytime.

11. The shells of the oysters remained open 94.4 per cent of the total time during daylight, and 93.8 per cent during the period of darkness. No correlation was found between the periods of closure of the shells and darkness.

12. Under favorable conditions neither tidal changes nor changes in the time of day affect the rate of feeding of oysters of Milford Harbor. These mollusks were found to be feeding all or most of the time when their shells remained open.

13. The results of this investigation do not lend any support to the generally accepted theory that the American oyster does not feed late at night and in the early morning, and is relatively inactive on the ebb tide.

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